

Spatial and environmental constraints on natural forest regeneration in the degraded landscape of Hong Kong

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Spatial and environmental constraints on natural forest regeneration in the degraded landscape of Hong Kong

Abstract

Tropical forests are the main reservoirs for global biodiversity and climate control. As secondary forests are now more widespread than primary forests, understanding their functioning and role in the biosphere is increasingly important. This includes understanding how they achieve stability, how they accumulate species and build biodiversity and how they cycle nutrients and carbon. This study investigates how we can restore tropical secondary forests to resemble high biomass, highly biodiverse and stable ecosystems seen today only in primary, undisturbed forests. The study used historic aerial photographs and recent high-resolution satellite images from 1945 to 2014 to map forest patches with five age categories, from 14-years to over 70-years, in Hong Kong's degraded tropical landscape. A forest inventory comprising 28 quadrats provided a rare opportunity to relate patterns of species composition at different stages during the succession with topographic and soil characteristics. The topographic variables accounted for 15 % of the variance in species abundance, and age of forest stands explained 29 %. Species richness rapidly increased after the first 15 years, but was lower in old-growth, than in medium age forest. This is attributed to the inability of late-successional species to disperse into the 'new, young' forests as the natural dispersal agents (birds, mammals) have been lost. Light-loving pioneers which are unable to tolerate the shade of older forests, cannot regenerate in their own shade, therefore species diversity declines after a few decades. For ecosystem restoration in tropical secondary forests, introduction of late-successional species is necessary to assist natural succession, given the absence of native fauna, seed dispersal agents, and the surrounding altered environment. We also show that remote sensing can play a pivotal role in understanding the recovery and functioning of secondary forest regeneration as its role in the biosphere is increasingly important.

Key Words: Remote Sensing; Spatial Patterns; Multi-temporal; Environmental constraints; Tropical Forest; Degraded Landscape; Succession: Secondary Forest; Biodiversity Conservation.

1. Introduction

The world's primary forests are rapidly disappearing. Forested areas decreased by 3.13% during the past quarter-century, from 4,128 m to 3,999 m ha., and today forest occupies only 30.6% of the world's land area. Of this, only 35% is primary forest. In the humid tropics, a 62% increase in deforestation from the 1990s to the 2000s is indicated by detailed analysis of multi-temporal Landsat data (Kim et al., 2015). A broad prediction of the future of tropical forest (Geist and Lambin, 2002) anticipates extensive agricultural encroachment into the old-growth forest due to an expected 2 billion increase in the population of tropical countries over the next few decades. Despite these pessimistic scenarios, secondary succession had regained 15 % of the area deforested globally during the 1990s and this regenerated secondary forest is becoming more abundant (Wright, 2005). The regeneration resulted from millions of hectares of the tropical landscape being abandoned following massive deforestation and large-scale agricultural activities, such as, in Myanmar (Sann et al., 2016), Brazil (Perz and Skole, 2003), Costa Rica (Helmer, 2000), Colombia (Faber-Langendoen, 1992), Singapore (Turner et al., 1997), Mexico (Guevara and Laborde, 1993), Puerto Rico (Grainger, 1988) and Venezuela (Saldarriaga et al., 1988). More recently, remote sensing-based estimates (Kim et al., 2015) also indicate accelerated forest gain in some parts of tropical Asia and decrease in deforestation in Brazil. Because most of the world's forests are now secondary, they have enhanced importance for climate control, catchment protection, biodiversity conservation and many ecological services (FAO, 2015).

The environmental determinants of ecological structure and composition have been widely examined (Anderson et al., 2011), as environmental conditions determine resource availability and influence community composition and structure (Punchi-Manage et al., 2013). The environmental conditions most commonly associated with the distribution of woody vegetation and floristic diversity in a landscape are topographic factors (Lovett et al., 2001) and soil properties (Arekhi et al., 2010). Furthermore, stability within a forest community tends to increase with progressive succession, as its structure and composition become more complex (Wang et al., 2006). For example, at a local scale, the

topography may define soil moisture conditions (Sukri et al., 2012) and distribution of nutrients (John et al., 2007), as valley bottoms and flatter areas are usually moister and richer in nutrients than ridge tops and steeper slopes (Balvanera et al., 2011) and this can influence the distribution of species. Also, topographic control of solar irradiance may affect the diversity of light-demanding, shade-tolerant species at a location (Larsen and Speckman, 2004). The physical and chemical properties of soil in a degraded landscape may also influence the growth and species composition of recovering secondary forests (Baldeck et al., 2016). Therefore, knowledge of environmental and spatial constraints on the floristic composition of recovering forests, are important for informing biodiversity conservation policies in disturbed tropical landscapes. Moreover, most of the remote sensing-based studies in tropical ecosystems has focused on patterns and processes of deforestation, degradation and recovery of the tropical forests (Lugo and Helmer, 2004). However, researchers have not given much attention to understanding the nature of forest being recovered and ecological implications of the recovering secondary forests. This is enabled by combining remote sensing-based assessments with field inventories of species composition (Guariguata and Ostertag, 2001). Therefore, this study was conducted to understand the effects of topography, soil and stand-age on species diversity during succession in a marginally tropical landscape.

The species diversity in Hong Kong's vascular plants is higher than in the whole of the UK, which has ~200 times the land area of Hong Kong (Dudgeon and Corlett, 2011). Most of Hong Kong's broad-leaved evergreen forests were removed centuries ago (Meachem, 1994). Nonetheless, restoration efforts the forests were commenced with large scale afforestation programs during the mid-19th century (Evan, 1992). However, all of the regenerated forest and plantations were destroyed due to fuelwood shortages during the Second World War. The current landscape of Hong Kong presents a rare example of tropical forest recovery since 1945 as a result of both natural succession and post-war large-scale plantations of fast-growing exotic species. This study documents and maps the age classes of the recovering forest over the 70 years, from 1945 to 2014, by time series analysis of remote sensing data comprising three sets of aerial photographs and two sets of high-resolution satellite images. This enables analysis of environmental and spatial constraints to species assemblage during the forest recovery process in the

severely degraded tropical landscape. The general objective of this study is to examine changes in species composition in the secondary forest succession across space and time. Specific objectives are to (i) understand the influence of topography on species composition and diversity, (ii) determine how floristic traits of the recovering forest are related to the age of the forest stands, and (iii) examine how the physical and chemical properties of soil influence the spatial and temporal patterns of forest succession.

The subsequent sections include the description of the study area in Section 2 which is followed by material and methods in Section 3. This includes a brief description of the forest age map, field inventory, environmental data preparation and data analysis comprising chronosequence analysis, Canonical Correspondence Analysis (CCA), Variation Partitioning and Multivariate Regression Tree. The results of the analysis are presented in Section 4 which is followed by a discussion of major findings (section 5). Finally, conclusions drawn from this study are given in Section 6.

2. Description of the study site

The study area covers ~2800 ha, comprising the Tai Mo Shan and Shing Mun Country Parks in Hong Kong located between 22° 09'N to 23° 37'N and 113°52'E to 114°30'E (**Figure 1**). Despite its tropical location, the climate of Hong Kong is regarded as sub-tropical due to strong seasonality of rainfall and temperature. The thirty-year (1981-2010) average temperature ranges from 16.3 °C in January to 28.8 °C in July while the average rainfall ranges between 24.7 mm in January and 456 mm in June. The study area has rugged topography, and steep convex slopes up to Hong Kong's highest peak at 957 m. Upper slopes are dominated by grasses, and woody vegetation increases with declining altitude towards valley bottoms. Temperature falls to freezing above 400 m a few times per decade (Dudgeon and Corlett, 2011).

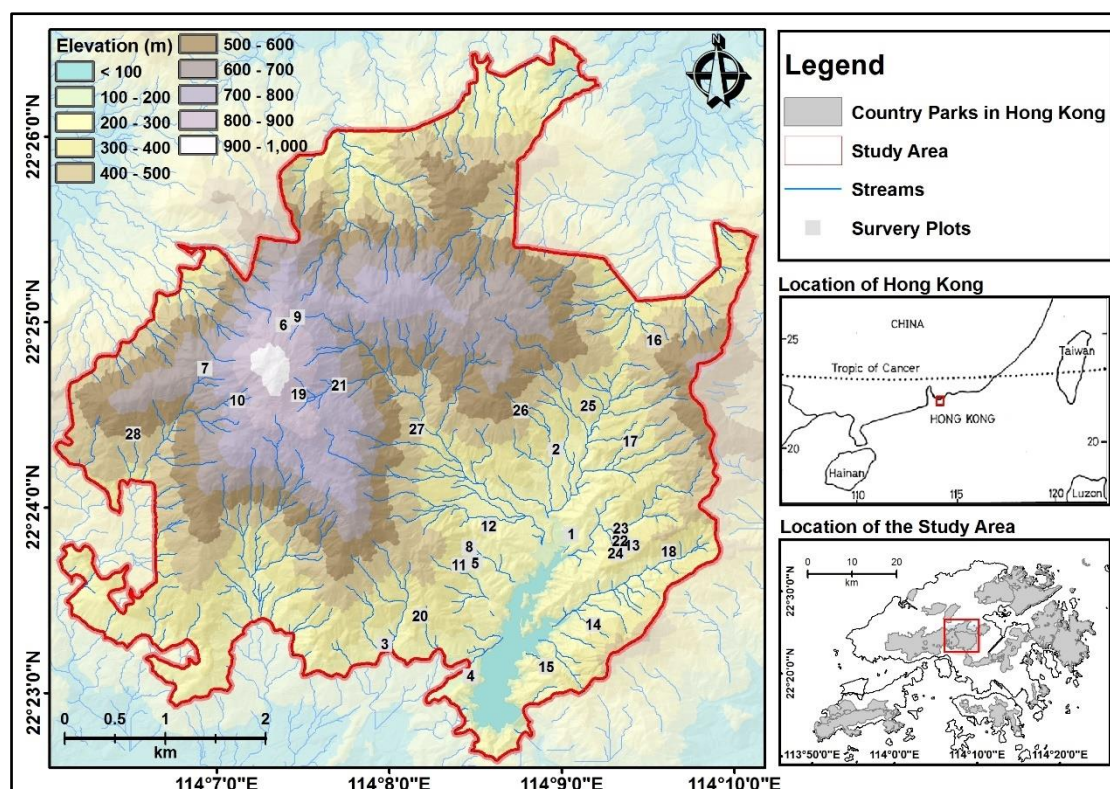


Figure 1 Location, topography and location of forest inventory plots in the study area

3. Materials and Methods

3.1 Sequential mapping of forest succession

Remotely sensed data comprising three sets of air photos of (1945, 1963 and 1989) as well as two satellite images (2001 and 2014) were used to map forest succession over 70 years, from 1945 to 2014. The aerial photographs were acquired at the scale of 1:40,000, 1:14,000 and 1:20,000, respectively, while the high-resolution satellite images were acquired by IKONOS and World View 2 in 2001 and 2014 at the spatial resolution of 1m and 0.5 m, respectively (Figure S1). A composite map of forest patches with five age categories, viz.: GT70 “forest older than 70-years (forest since 1945)”, LT70 “younger than 70-years (forest since 1963)”, LT52 “younger than 52-years (forest since 1989)”, LT26 “younger than 26-years (forest since 2001)”, and LT14 “younger than 14-years (forest since 2014)” was created, to collect and analyze species data along the chronosequence of forest succession. All the images were geometrically corrected, and orthorectified using a digital orthophoto and a 2 m Digital Elevation Model of Hong Kong obtained from the Lands Department of Hong Kong. For a detailed

description of methods applied for remote sensing data processing and habitat mapping, see Abbas et al., (2018, 2016).

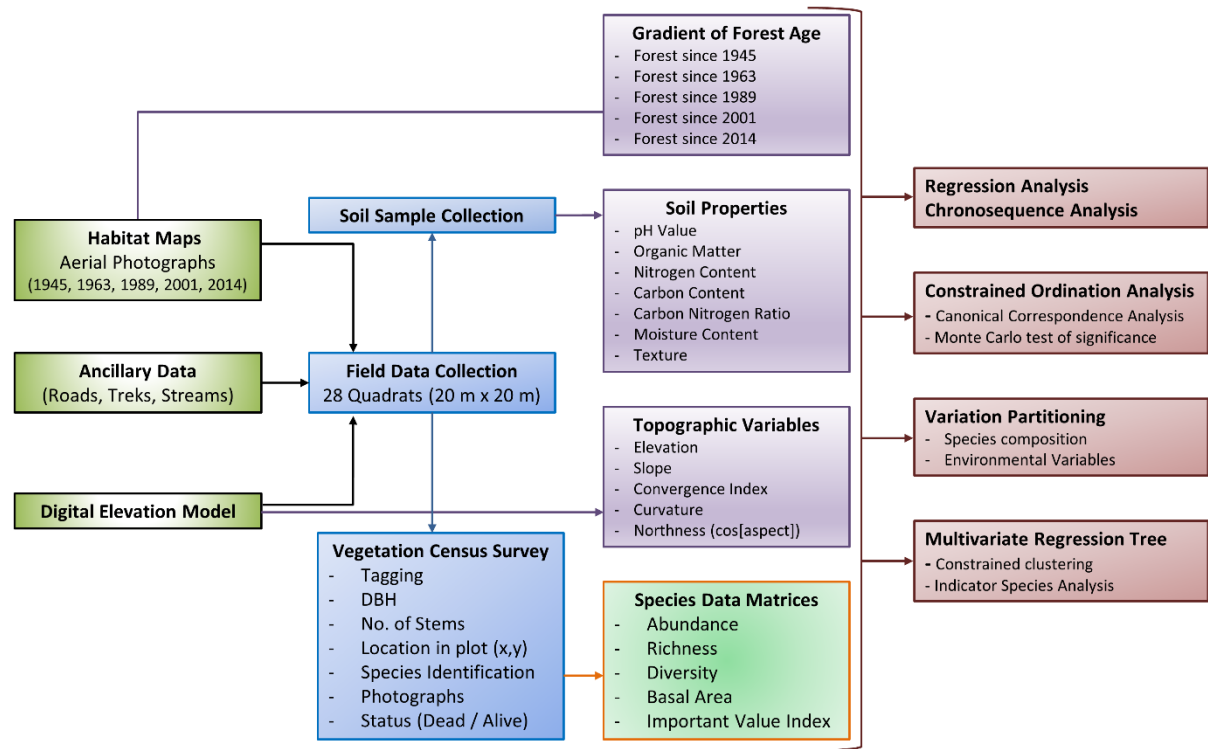


Figure 2 A flow chart of the methodology applied in this study

3.2 Species data collection

Sequential mapping of forest recovery was followed by *in-situ* vegetation census data and soil samples collection between March 2015 and June 2016. Plots were located by stratified random sampling, due to ruggedness of the landscape. In total, 28 plots located in forest patches belonging to the five age classes ('GT70', 'LT70', 'LT52', 'LT26' and 'LT14') and covering a total area of 1.12 hectares were established, with an attempt to sample at 200 m altitudinal intervals, and in all cardinal directions (**Figure 1**). Considering the fragmented nature of forest in the study area, a sampling size of 20 m by 20 m was used, to ensure physiognomic uniformity of each plot as demonstrated by Lee et al., (2007, 2005), and Zhuang and Corlett (1997). Within each sample plot, measurements included Diameter at Breast Height (DBH), number of stems, and status (Dead or Alive). High-quality digital photographs were taken for species identification, following the classification of flowering plants by the Angiosperm

Phylogeny Group (APGIII, 2009). Only woody plants were identified, ignoring herbs, grasses, and ferns.

3.3 Environmental variables

Five topographic variables were derived from a 2 m DEM, including; elevation, slope, northness (cosine [aspect]), convergence index, and curvature. A correlation matrix of the variables was computed to examine multicollinearity among the different topographic variables. The selected variables were independent at the threshold level of $r < 0.50$. Additionally, composite soil samples were taken from each plot at 20 cm depth. The samples were analyzed for percentages of sand, silt, clay, organic matter, carbon, and nitrogen, as well as for pH and moisture content.

3.4 Data analysis

Two vegetation data matrices comprising species' basal area metrics and species' density metrics were computed from the vegetation census data. The diversity of communities was measured by species abundance "the total number of plants of any species occurring in a community", species richness "the total number of species occurring in a community", Shannon's Diversity Index H' "the components of richness and abundance of species in a plant community" (Magurran, 1988), and Pielou's Evenness Index J "an index of uniformity of species abundance which indicates either most individuals belong to fewer species or are equally abundant". A simple linear regression analysis was performed to determine the association between environmental constraints and the distribution of floristic traits (Table 1).

3.4.1 Canonical Correspondence Analysis (CCA)

CCA is a constrained ordination which combines direct (regression) and indirect (ordination) gradient analysis to determine how environmental variations (topography, soil, stand-age) influence species composition across the landscape (Legendre and Legendre, 2012). CCA was performed by forward selection of the variables followed by the 1000 random permutations of the Monte Carlo test (at the 5 % confidence level) to evaluate variance explained by each variable, the significance of the variable and the pseudo F -value. To avoid multicollinearity, environmental variables with larger variance inflation factors (VIFs), $VIF > 10$, were omitted before performing CCA. The analysis was executed using the 'vegan' package in R.

3.4.2 Variation Partitioning

Variation partitioning was performed to quantify the fraction of variation in the species distribution contributed by each set of environmental variables (topography, soil, and stand-age) (Baldeck et al., 2016). Variation partitioning splits the total variation in species composition into the fractions uniquely explained by each set of variables (for our analysis - topography, soil, and age), as well as variance explained by each combination of the explanatory variable set. It was performed in R using the ‘vegan’ package.

3.4.3 Multivariate Regression Tree (MRT) and indicator species analysis

A multivariate regression tree (MRT) approach was applied, to floristically group similar sites by species assemblages, in association with the environmental variables. The species abundance matrix was square-root transformed and the sum of squares (Euclidean distance) MRT (SS-MRT) was used for splitting (De’ath, 2002; DeVantier et al., 2006) (De’ath, 2002; DeVantier et al., 2006) (De’ath, 2002; DeVantier et al., 2006) (De’ath, 2002; DeVantier et al., 2006) (De’ath, 2002; DeVantier et al., 2006). The tree was pruned by using the 1-SE rule, which resulted in a tree size of seven (De’ath, 2002). Furthermore, “indicator species analysis” was performed to investigate the statistically significant indicator species (Legendre et al., 2009) which best characterized the groups. The analysis was performed using the ‘mvpart’, ‘labdsv’, and ‘MVPARTwrap’ packages in R.

4. Results

In the vegetation census survey of the 28 plots distributed in the five age-groups of forest patches, more than 8500 plants of ≥ 1 cm DBH were recorded. The total number of species identified in the plots was 229, comprising 63 families.

4.1 Chronosequence analysis of species data and soil samples

Analysis of species data along the chronosequence showed a consistent increase in total stand basal area. However, after 70 years of succession the stand basal area of secondary forests had reached only half that of old-growth forest stands (**Figure 3**). The proportion of dead trees significantly decreased after ~50 years of succession, suggesting some reduction in species turnover. Species richness and

abundance were also observed to vary as a function of stand age, with both increasing over the first 50 years of succession, but then reducing in the old-growth forest (**Figure 3**). Soil analysis shows that the C:N decreases with increasing forest age and that higher elevation soil tends to have a significantly higher C:N ratio, than in lower elevation forest (**Table 2**).

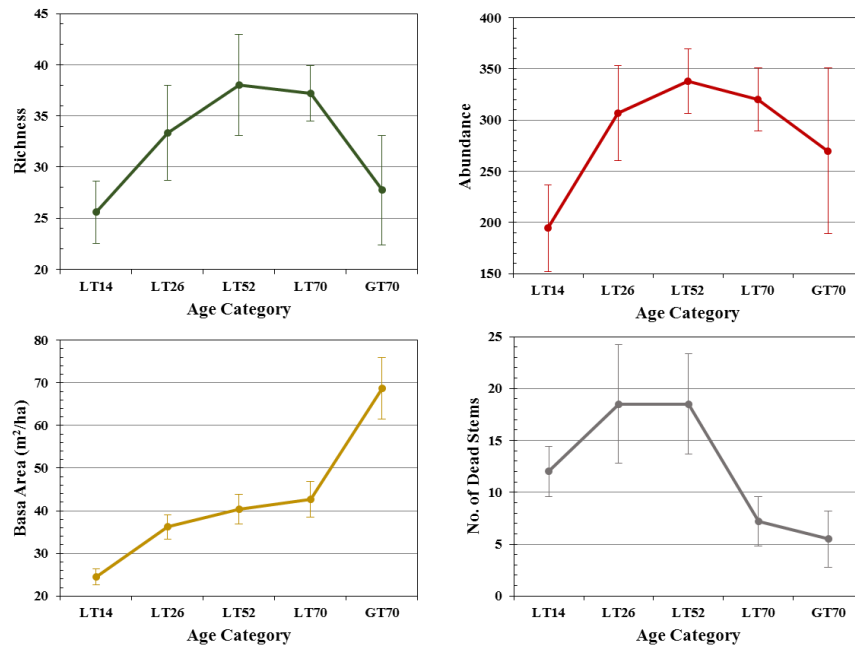


Figure 3 Floristics traits of the secondary forest along the successional stages

Table 1 Soil properties along the chronosequence of forest succession. Values are averages (and standard deviation) for all plots in each successional stage. The significant difference was analyzed using ANOVA at the 0.05 significance level and significantly different soil properties are marked with ‘ * ’.

Soil Property	Age Categories					Elevation Division	
	LT14	LT26	LT52	LT70	GT70	Lowland (≤ 467.5m)	Montane (>467.5m)
pH	4.54 ± 0.19	4.48 ± 0.08	4.50 ± 0.09	4.60 ± 0.14	4.50 ± 0.08	4.51 ± 0.13	4.56 ± 0.08
Organic Matter (%)	3.94 ± 1.55	4.03 ± 1.76	3.21 ± 0.63	3.74 ± 0.86	3.75 ± 0.66	3.50 ± 1.03	4.26 ± 1.34
Nitrogen (%)	0.16 ± 0.09	0.14 ± 0.05	0.14 ± 0.03	0.16 ± 0.06	0.17 ± 0.03	0.15 ± 0.05	0.14 ± 0.06
Moisture Content	24.30 ± 2.78	22.40 ± 1.03	24.91 ± 2.46	22.94 ± 1.49	24.88 ± 1.89	23.74 ± 2.26	24.40 ± 2.03
Carbon (%)	7.18 ± 2.06	7.63 ± 2.10	6.80 ± 1.03	7.22 ± 1.85	7.30 ± 1.16	7.17 ± 1.53	7.26 ± 1.82
C : N *	27.20 ± 5.93	27.98 ± 5.47	24.21 ± 7.67	24.18 ± 6.34	21.75 ± 1.54	<u>*23.07 ± 4.11</u>	<u>*31.57 ± 6.83</u>
Sand (%)	87.40 ± 4.34	86.17 ± 6.01	84.63 ± 5.07	86.20 ± 3.11	88.50 ± 1.92	85.57 ± 4.37	88.43 ± 4.28
Silt (%) *	6.00 ± 2.83	6.33 ± 2.94	7.50 ± 3.16	6.00 ± 1.41	6.00 ± 0.00	<u>*7.05 ± 2.33</u>	<u>*4.86 ± 2.27</u>
Clay (%)	6.60 ± 1.67	7.50 ± 3.78	7.88 ± 2.23	7.80 ± 1.92	5.50 ± 1.92	7.38 ± 2.50	6.71 ± 2.43

4.2 Association of floristic traits with environmental variables

Pearson's correlation coefficient was calculated to determine the association among environmental variables (topography and soil) and the floristic traits (species abundance, richness, diversity and evenness) (**Table 2**). Among the environmental variables, only elevation and soil indicate a significant association with the floristic traits ($p \leq 0.1$). Species abundance was inversely correlated with both elevation ($r = -0.49, p \leq 0.01$) and the carbon-nitrogen ratio ($r = -0.37, p \leq 0.1$), i.e., fewer plants towards higher elevations as well as fewer plants with an increase in the carbon-nitrogen ratio. Diversity and evenness were positively affected by elevation ($r = 0.328, p \leq 0.1$; $r = 0.516, p \leq 0.01$), showing greater diversity and evenness with increasing elevation and increasing carbon-nitrogen ratio ($r = 0.34, p \leq 0.1$; $r = 0.42, p \leq 0.05$). Evenness also showed a significantly positive link with soil organic matter ($r = 0.33,$

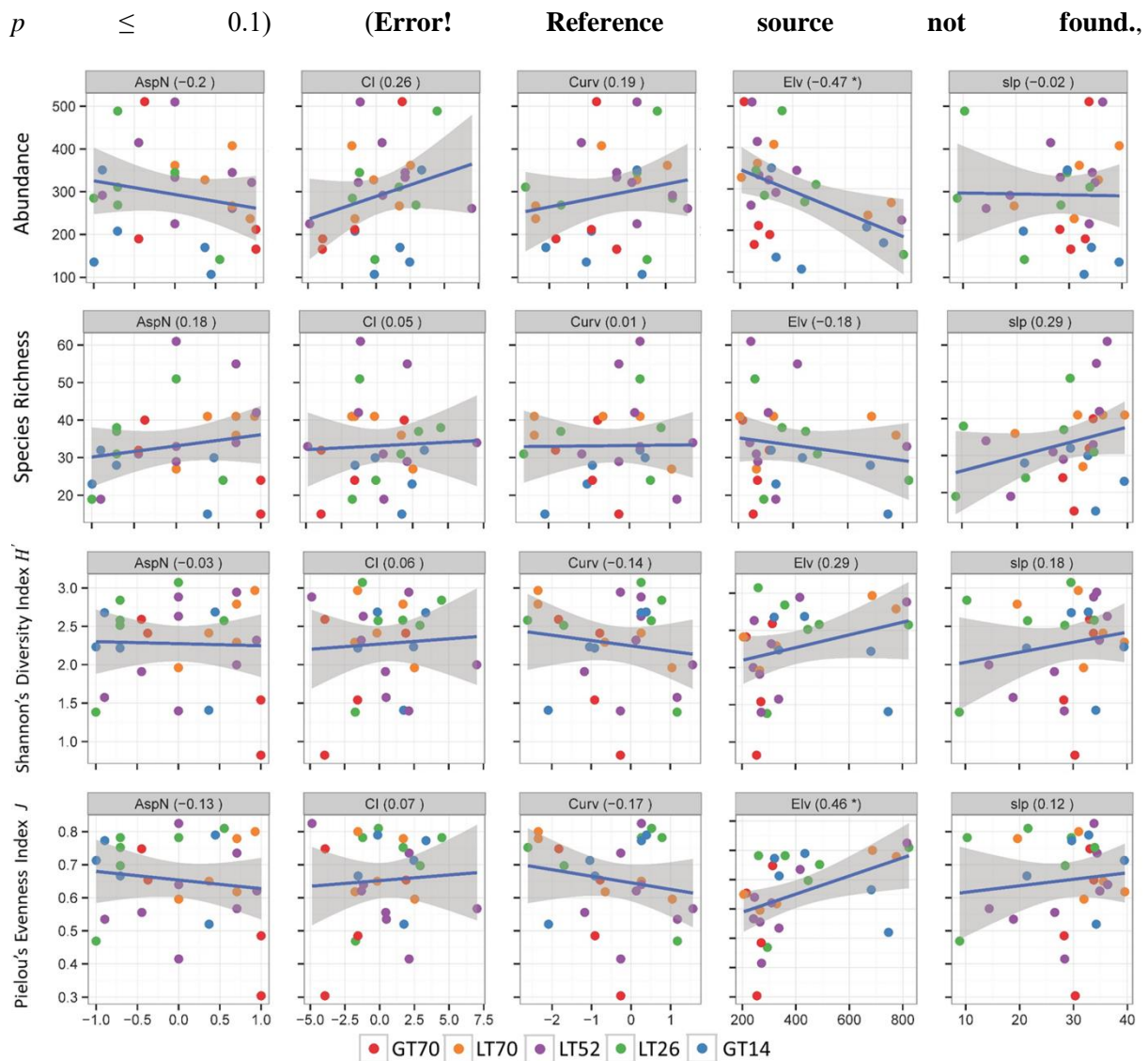


Figure 4). Although correlations of species richness with slope suggested more species per forest stand on steeper slopes, ($r = 0.31$), the relationship was not significant (**Table 2**,

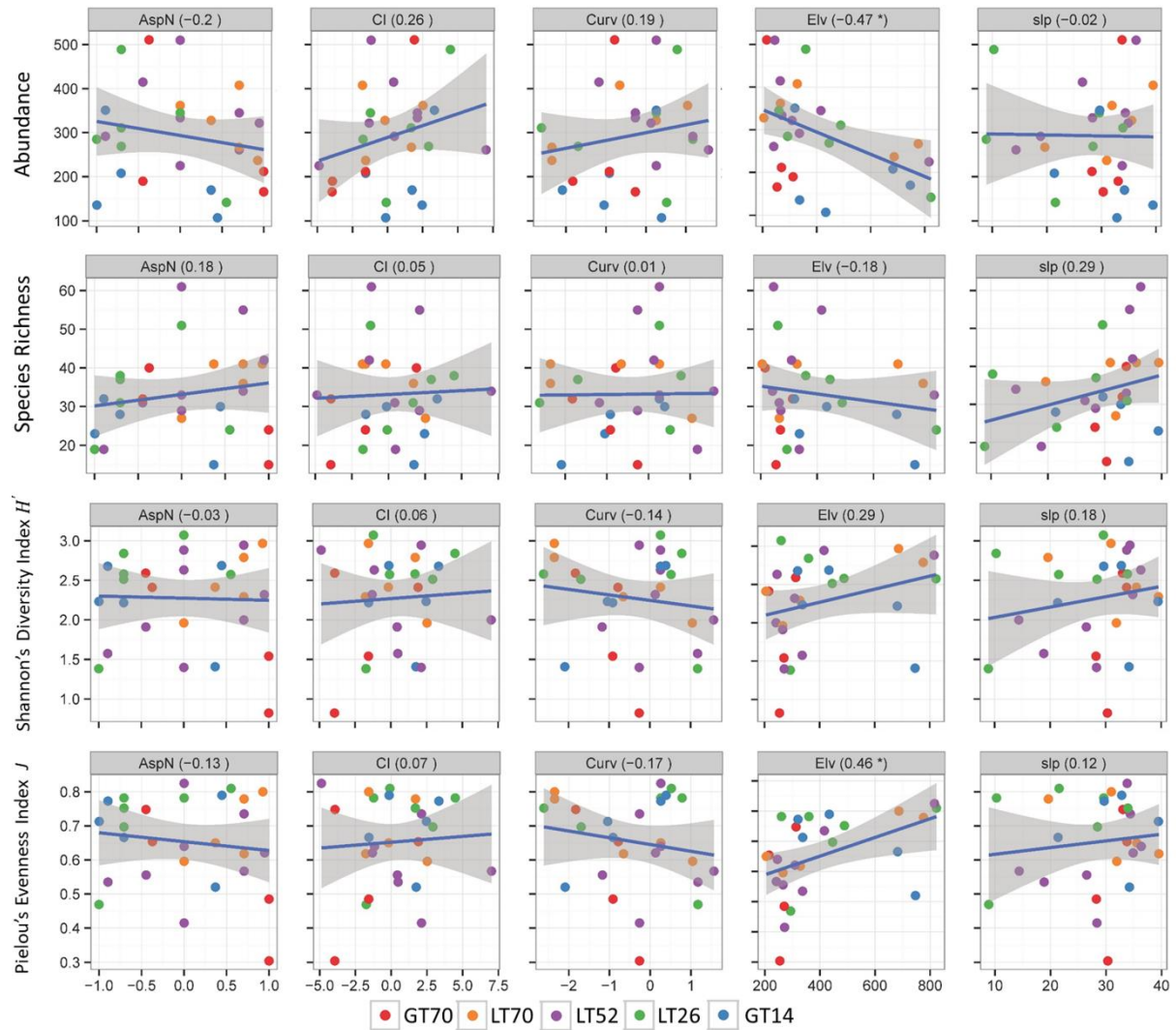


Figure 4).

Table 2 Pearson correlation between diversity indices and the environmental variables

Variable	Abbreviation	Richness	Abundance	Shannon-Wiener Index	Evenness
Cosine of Aspect	AspN	0.19	-0.11	-0.01	-0.15
Elevation	Elv	-0.19	-0.49***	0.328*	0.516***
Slope	slp	0.31	0.05	0.17	0.10
Curvature	Curv	0.01	0.19	-0.14	-0.18
Convergence Index	CI	0.05	0.26	0.01	0.02
pH	pH	0.17	-0.278	0.16	0.12
Organic Matter	OM	-0.14	-0.22	0.18	0.333*

Nitrogen	N	-0.14	0.03	-0.06	0.03
Moisture	M	-0.12	-0.13	-0.29	-0.29
Carbon	C	-0.24	-0.19	0.09	0.21
Carbon Nitrogen Ratio	C:N	0.02	-0.369*	0.335*	0.419**
Texture	S	-0.14	-0.19	0.08	0.19

Significance levels: *** ($p \leq 0.01$), ** ($p \leq 0.05$), * ($p \leq 0.1$)

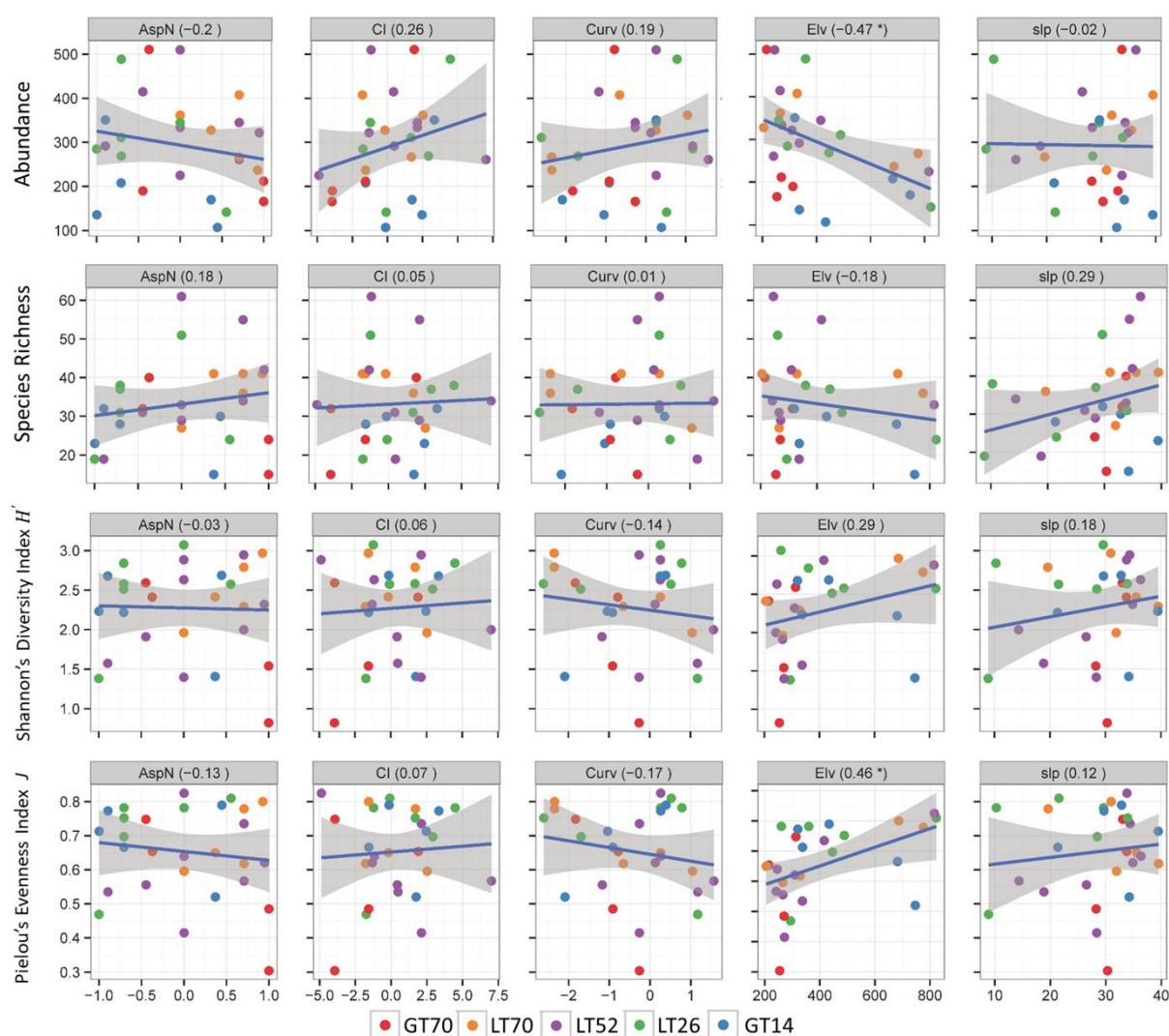


Figure 4 Association of the topographic variables and the floristic traits

4.3 Canonical Correspondence Analysis (CCA)

Prior to the ordination analysis, the following environmental variables were forward selected based on significance and variance inflation factors: five topographic variables - elevation (Elv), aspect (AspN), slope (slp), convergence index (CI), and curvature (Curv), two soil variables - carbon (C), and carbon-nitrogen ratio (C:N), and one categorical variable – age of sample sites (Age). This combination of

variables explained 56.5% of the total variance in the species composition and a Monte Carlo permutation test (with 1000 permutations) indicated significant vegetation – environment relationships distinguished by all axes ($F\text{-value} = 1.888$, $P = 0.009$). The first two axes of the CCA explained 22.1% of the variance in species composition out of which 11.73 % was explained by the first axis ($p = 0.009$: the Monte Carlo permutation test with 1000 permutations) and the second axis explained 10.4%. The first axis was positively correlated with elevation while the second axis was negatively correlated with curvature and convergence index, and as well, indicated a positive association with aspect (**Error! Reference source not found.**). The vectors in the ordination diagram show the influence of environmental factors on the species composition. The relative significance of the factors is indicated by the length of the vectors, and their angles formed with the axes of the ordination graph exhibit the correlations between the variables and the axes. The sample sites at high elevation are distinguishable by their placement at the top right corner of the ordination diagram and are differentiated from the other sites due to abundance of species such as *Myrsine seguinii*, *Camellia caudate*, *Ligustrum japonicum*, *Eurya nitida*, *Eurya macartneyi*, and *Ilex viridis* (**Error! Reference source not found.**). The oldest sites, all located at lower elevations, at the top left side of the diagram, are distinguished by abundance of late successional tree species such as *Cryptocarya chinensis*, and *Elaeocarpus chinensis*. The remaining sites located in the middle and bottom of the diagram are marked by early or mid-successional species such as, *Psychotria asiatica*, *Aporosa octandra*, *Machilus gamblei*, *Machilus chekiangensis*, *Diospyros morrisiana*, *Machilus breviflora*, *Schefflera heptaphylla*, *Acronychia pedunculata*, *Desmos chinensis*, *Sterculia lanceolate*, *Syzygium hancei*, *Daphniphyllum calycinum*, *Ilex asprella*, and *Garcinia oblongifolia*.

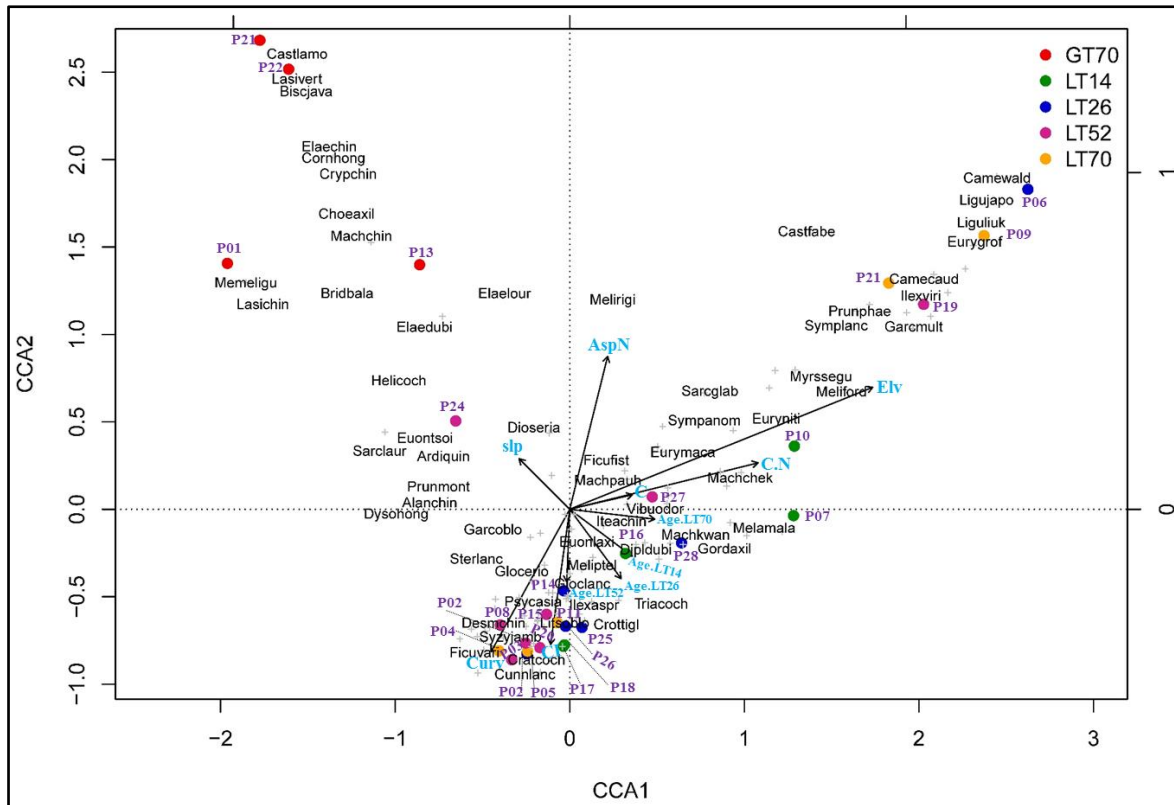


Figure 5 CCA ordination diagram showing the relationship between abundant species and the environmental variables. Sites are represented by filled circles, with colours corresponding to the age of the site, and species are shown by “+” sign in grey colour and overlaid with =abbreviated names of dominant species.

Elv = Elevation, AspN = Aspect (northness), slp = Slope, Curv = Curvature, CI = Convergence Index, C.N = Carbon – Nitrogen Ratio, C = Carbon, GT70 = greater than 70-year old forest (forest since 1945), LT70 = less than 70-year old forest (forest since 1963) LT52 = less than 52-year old forest (forest since 1989), LT26 = less than 26-year old forest (forest since 2001), and LT14 = less than 14-year old forest (forest since 2014). Alanchin = *Alangium chinense*, Ardiquin = *Ardisia quinquegona*, Biscjava = *Bischofia javanica*, Bridbala = *Bridelia balansae*, Camecaud = *Camellia caudata*, Camewald = *Camellia sinensis* var. *waldenae*, Castfabe = *Castanopsis faberi*, Castlamo = *Castanopsis lamontii*, Choeaxil = *Choerospondias axillaris*, Cornhong = *Cornus hongkongensis*, Cratcoch = *Cratoxylum cochinchinense*, Crottigl = *Croton tiglium*, Crypchin = *Cryptocarya chinensis*, Cunnlanc = *Cunninghamia lanceolata*, Desmchin = *Desmos chinensis*, Dioseria = *Diospyros eriantha*, Dipldubi = *Diplospora dubia*, Dysohong = *Dysoxylum hongkongense*, Elaelour = *Elaeagnus loureiroi*, Elaechin = *Elaeocarpus chinensis*, Elaedubi = *Elaeocarpus dubius*, Euonlaxi = *Euonymus laxiflorus*, Euontsoi = *Euonymus tsoi*, Eurygrof = *Eurya groffi*, Eurymaca = *Eurya macartneyi*, Euryntiti = *Eurya nitida*, Ficufist = *Ficus fistulosa*, Ficuvvari = *Ficus variegata*, Garcmult = *Garcinia multiflora*, Garcoblo = *Garcinia oblongifolia*, Gloclerio = *Glochidion eriocarpum*, Gloclwig = *Glochidion wrightii*, Gordaxil = *Gordonia axillaris*, Helicoch = *Helicia cochinchinensis*, Ilexaspr = *Ilex asprella*, Ilexviri = *Ilex viridis*, Iteachin = *Itea chinensis*, Lasichin = *Lasianthus chinensis*, Lasivert = *Lasianthus verticillatus*, Ligujapo = *Ligustrum japonicum*, Liguliu = *Ligustrum luikiuense*, Litsoblo = *Litsea rotundifolia* var. *oblongifolia*, Machchek = *Machilus chekiangensis*, Machchin = *Machilus chinensis*, Machkwan = *Machilus kwangtungensis*, Machpauh = *Machilus pauhoi*, Melamala = *Melastoma malabathricum*, Meliptel = *Melicope pteleifolia*, Meliford = *Meliosma fordii*, Melirigi = *Meliosma rigida*, Memeligu = *Memecylon ligustrifolium*, Myrssegu = *Myrsine seguinii*, Prunmont = *Prunus arborea* var. *montana*, Prunphae = *Prunus phaeosticta*, Psycasia = *Psychotria asiatica*, Sarcglab = *Sarcandra glabra*, Sarclaur = *Sarcosperma laurinum*, Sterlanc = *Sterculia lanceolata*, Sympanom = *Symplocos anomala*, Symplanc = *Symplocos lancifolia*, Syzyjamb = *Syzygium jambos*, Triacoch = *Triadacochinchinensis*, Vibudor = *Viburnum odoratissimum*.

4.4 Variation partitioning

Variation partitioning can facilitate understanding of the relative influences of topographic filtering, the effect of soil fertility, and age-groups on species assemblage processes. In this study, variation partitioning was used to quantify the relative importance of the different environmental variables

including topography (elevation, aspect (northness), slope, convergence index and curvature), soil (carbon-nitrogen ratio) and age, in explaining the variance in species composition (**Figure 6**). The highest proportion of the variance in species composition was explained by age of forest stands (29%) followed by topography (15%) and soil (1%). The combination of soil and topography explained 10% of the variance in species composition. In total, 56% of the variance was explained by the environmental variables (age, topography and soil) while the remaining 44% of the variance remained unexplained (**Figure 6**). Thus, we can infer that species composition patterns in the landscape are related to topography, which is a static variable, and successional stage of forest stands, which is a dynamic variable. In contrast, the soil variable played a less significant role in the distribution of species.

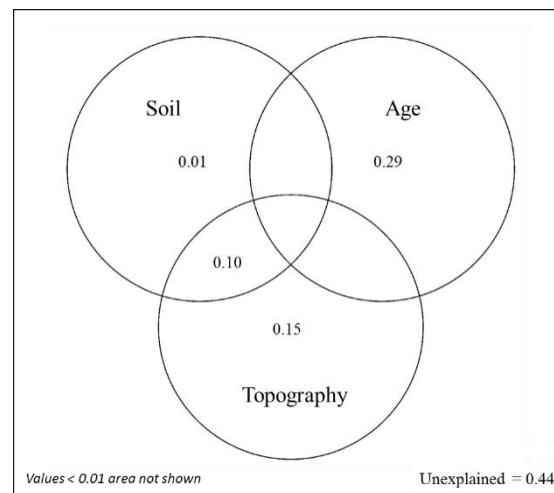


Figure 6 Partitioning of the variation of species explained by the environmental variables

4.5 Multivariate Regression Tree and indicator species

Sites were grouped by MRT based on species composition and environmental variables of the sites. A tree with seven terminal nodes was created, with splits based on four explanatory variables (elevation, age, convergence index and curvature) (**Figure 7**). The cross-validation relative error of the MRT was 0.86 and the tree explained 64.5% of the standardized species variance. Splits were primarily governed by elevation and age categories. Elevation governed the first split (breakpoint = 467.5) accounting for 20.9% of the species variance. The second major split was determined by the age at node-3, which explained an additional 24.6% of the variance in species composition (**Figure 7**). The total additional variance explained by the other splits was 19%. The discriminant species for the first split was

295 *Psychotria Asiatica*, which was the dominant species in the right-hand branch of the tree along with
296 *Aporosa octandra* and *Garcinia oblongifolia*. These species also had minimum presence on the left-
297 hand branch of the tree which represented species at higher elevations (Elv > 467 m). The left-hand
298 branch of the tree (higher elevations) was dominated by *Machilus thunbergii*, *Machilus chekiangensis*,
299 and *Myrsine seguinii*, and *Machilus chekiangensis* became the discriminant species to form groups A
300 and B. Similarly, the right-hand branch of the tree was split to form the five groups C, D, E, F and G
301 (**Figure 7**). Furthermore, indicator species were analyzed for all the groups forming the seven trinomial
302 nodes of the tree. For example, group A representing two young pioneer sites at high elevations (P07
303 and P10) had three significant indicator species, namely *Melastoma malabathricum*, *Machilus*
304 *chekiangensis*, and *Machilus pauhoi*, whereas group G contained 3 sites representing young forest at
305 low elevations (P25, P26, and P28) and had five significant indicator species namely *Pavetta*
306 *hongkongensis*, *Ficus variolosa*, *Rhodomyrtus tomentosa*, *Glochidion wrightii* and *Diospyros*
307 *morrisiana* (**Figure 7**).

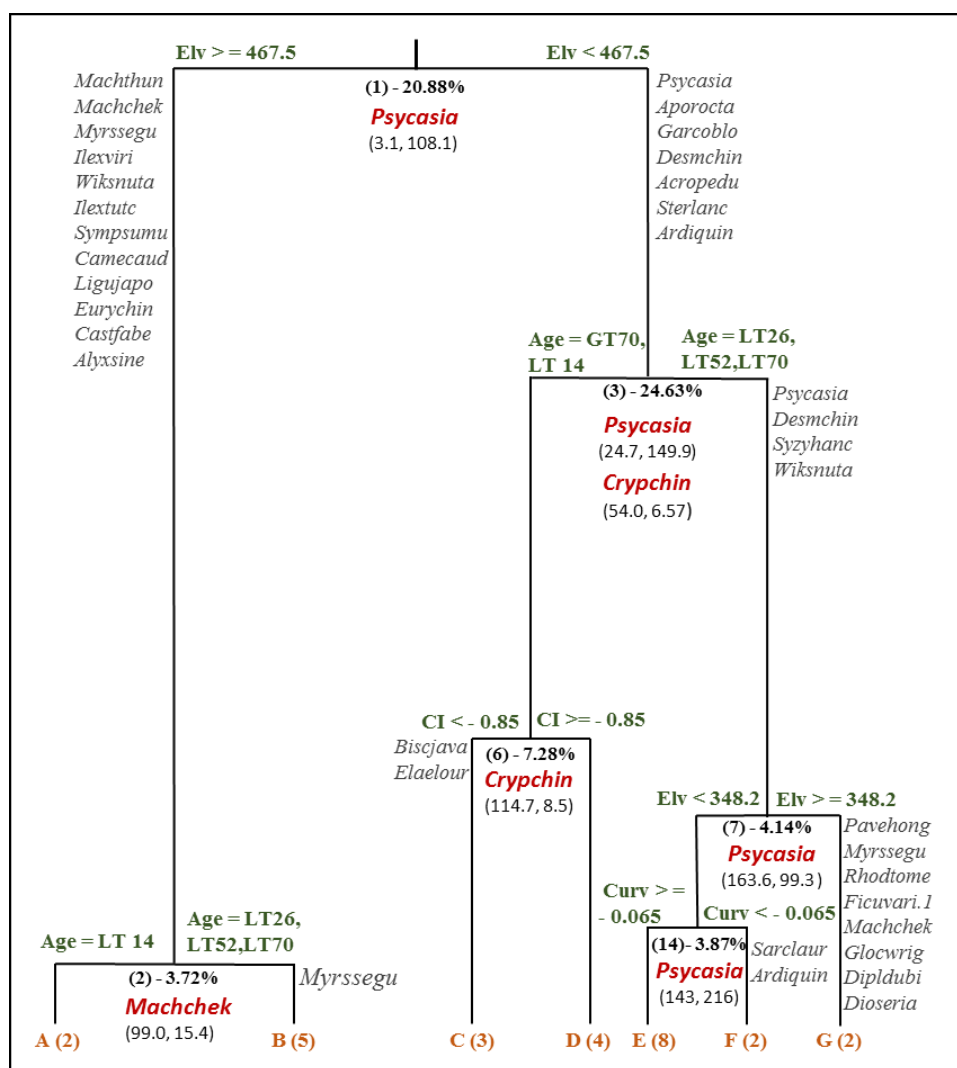


Figure 7 Regression tree developed from the Multivariate regression tree analysis

The species abundance matrix was square-root transformed and Euclidean distance was used for splitting. Variation explained by each node is given under the node, breakpoints of an explanatory variable at every leaf of the node are in green font, significant indicator species at each node are mentioned on the left and the right of the node and discriminant species at the node is also given in italic and red font. Final partitioning cluster is indicated with letter A to G with the number of site in the bracket. (Variation Explained (R²): 64.5 %; Variation not Explained (Error): 35.5 %; Cross-Validation Relative Error (CVRE): 0.857; Standard Error (SE): 0.131. Acropedu = *Acronychia pedunculata*, Alyxsine = *Alyxia sinensis*, Aporocta = *Aporosa octandra*, Ardiquin = *Ardisia quinquegona*, Biscjava = *Bischofia javanica*, Camecaud = *Camellia caudata*, Castfabe = *Castanopsis faberi*, Crypchin = *Cryptocarya chinensis*, Desmchin = *Desmos chinensis*, Dioseria = *Diospyros eriantha*, Dipldubi = *Diplospora dubia*, Elaelour = *Elaeagnus loureiroi*, Eurychin = *Eurya chinensis*, Ficuvvari.1 = *Ficus variolosa*, Garcoblo = *Garcinia oblongifolia*, Glocwrig = *Glochidion wrightii*, Ilextut = *Ilex tutcheri*, Ilexviri = *Ilex viridis*, Ligujaipo = *Ligustrum japonicum*, Machchek = *Machilus chekiangensis*, Machthun = *Machilus thunbergii*, Myrssegu = *Myrsine seguinii*, Pavehong = *Pavetta hongkongensis*, Psycasia = *Psychotria asiatica*, Rhodtome = *Rhodomyrtus tomentosa*, Sarclaur = *Sarcosperma laurinum*, Sterlanc = *Sterculia lanceolata*, Sympsumu = *Symplocos sumuntia*, Syzyhanc = *Syzygium hancei*, Wiksnuta = *Wikstroemia nutans*

5. Discussion

5.1 Influence of stand age and soil conditions

The chronosequence of the total basal area along the stand-age sequence can increase asymptotically, or peak at an intermediate stage (Guariguata and Ostertag, 2001), as observed by Denslow (2000) during secondary forest succession in Panama. In this study, the increased basal area followed this asymptotic pattern (**Figure 3**), but after 70 years of succession, it had reached only the half that of old-growth forest stands, contrary to Denslow's (2000) reported equality with old-growth stands. This may be due to lower availability of soil nutrients (Denslow, 2000), as we observed average N content of 0.14 % compared to 0.19 % reported by Fang et al (2009) in an old-growth forest in the nearby Dinghushan forest reserve in southern China. Similarly, higher concentrations of nutrients were found in older stands in similar forest type in eastern China (Yan et al, 2006). The low nutrient status in our study is also suggested by an observed C/N ratio of 27.1 compared to 22.1 in the Dinghushan old-growth forest. In addition to loss of nutrients from centuries of deforestation, massive soil erosion on the steep slopes has no doubt contributed to the low soil nutrient status, and thus to the slow rate of biomass accumulation. When analyzed by age of forest stand (**Figure 3**), species richness and abundance are positively correlated and follow the "intermediate disturbance hypothesis" of Connell, (1978) which is indicated by a "hump-backed curve (Pausas and Austin, 2001)". Thus a steady increase in species richness and abundance are evident during earlier successional stages, reaching a maximum value at an intermediate stage at approximately 50 years, and falling thereafter (**Figure 3**). This chronosequence pattern is contrary to 'succession models (Peet, 1992) which suggest an asymptotic increase to maximum species diversity, exemplified by Saldarriaga et al. (1988) in the recovering forests of Colombia and Venezuela. As succession proceeds to old-growth forest, the decline in species diversity in Hong Kong's secondary forests may be explained by the absence of later successional forest species which can grow under the shade of well-established forest pioneers, and is not surprising given the absence of specialist forest fauna, combined with the poor dispersal abilities of shade-tolerant species. Nevertheless, the observed decrease in the number of species with the progress of succession could be caused by sampling errors

or by the exclusion of certain species, and this can be clarified by increased numbers of inventory plots in future studies.

5.2 Influence of topography

The study supports the strong influence of topographic variables on species distribution observed in other studies (Lovett et al., 2001; Punchi-Manage et al., 2013). Among the topographic variables, elevation and curvature were the main drivers of species distribution patterns. The fundamental hypothesis of environmental filtering in community assemblage in tropical forests (Taylor et al., 1990) is supported by our data showing a significant influence of topography on species composition, which illustrates habitat filtering at a local community scale. Thus, species abundance notably decreased towards higher elevations possibly due to our observed increase in the C:N ratio, suggesting lower soil nutrient status. This would also support our observation of higher species diversity at higher elevations, as explained below. Zhuang and Corlett, (1996) also documented higher species diversity of secondary forest in the uplands of Hong Kong but attributed this mainly to inaccessibility and lower human impact. Similar observations were documented by Liu et al., (2014) in a tropical forest in southwest China. Our observation of an increasing trend in species diversity along with increasing C:N ratio supports the findings of Nadeau and Sullivan, (2015), from mature tropical forests in Costa Rica. Thus it has been observed that in tropical forests high species diversity tends to associate with poor soil and lower fertility (Peña-Claros et al., 2012). In these ecosystems, the highest species richness occurs under poor growth conditions where nutrient-poor soil (leached due to the chemical weathering under high temperature and rainfall (Tilman et al., 1996)) does not allow the dominance of a few species. Instead, opportunistic competition is set up, whereby the fittest to survive the impoverished environment compete for survival. On the other hand, nutrient-rich soil enables faster growth rates that allow rapid competitive exclusion. Furthermore, in poor soil conditions, a species-rich decomposer web of bacteria, fungi and soil mesofauna acts as an effective filter retaining the nutrients being leached by rainwater and thus avoiding nutrient loss (Tilman et al., 1996). The plants also retain and recycle nutrients, minimizing nutrient loss and so the leaf litter is usually poor in N and other nutrients. This suggests that most of the nitrogen and nutrients are taken up by the plants at the moment nutrients are released by

decomposition (Terborgh, 1992). Therefore carbon, being a product of plant decomposition, will be high relative to nitrogen (Nadeau and Sullivan, 2015).

Elevation also exerts a strong influence on species composition. Both the constrained ordination and regression tree classifications indicate that elevation, with a breakpoint at 467 m, clearly defines two different parallel successional trajectories, with different floristic composition. At lower elevations species ordination (**Error! Reference source not found.**) shows a floristic trend from light-demanding pioneers, such as *Aporosa octandra*, *Acronychia pedunculata*, *Daphniphyllum calycinum*, *Diospyros morrisiana*, *Ficus variolosa*, *Psychotria asiatica*, *Schefflera heptaphylla*, *Sapium discolor*, and *Sterculia lanceolate*, to large dominant species in older sites including *Bischofia javanica*, *Choerospondias axillaris*, *Cryptocarya chinensis*, *Elaeocarpus chinensis* and *Sarcosperma laurinum*. Higher elevations included some species thought to have mainly sub-tropical distributions. They were first colonized with light-demanding pioneer species such as *Gordonia axillaris*, *Machilus chekiangensis*, *Melastoma malabathricum*, and, then later dominated by species including *Camellia caudate*, *Eurya chinensis*, *Ilex viridis*, *Ligustrum japonicum*, *Myrsine seguinii*, *Machilus breviflora* and *Symplocos sumuntia*, of which *Ilex* and *Symplocos* are thought to be more sub-tropical genera, while *Gordonia*, *Eurya* and *Camellia* belong to the Theaceae family which is also thought to be sub-tropical. Similar patterns of parallel forest recovery along the elevational gradient were observed by Aide et al. (1996) in the abandoned pastures of northeast Puerto Rico.

In the present study, the altitudinal breakpoint in the floristic composition may result from damage by frost events. During a cold spell in January 2016, temperatures fell to -6°C at 950 m on Tai Mo Shan. Field visits in February to June 2016, showed notable stress on vegetation starting at 400 m, and increasing upwards. Above 600 m even large and mature native trees of *Canarium album*, *Carallia brachiata*, *Ficus ssp.*, *Garcinia oblongifolia*, *Litsea ssp.*, *Mallotus paniculatus*, and *Schefflera heptaphylla*, as well the exotics *Acacia confusa*, *Eucalyptus spp.* and *Lophostemon confertus* were partially or completely lost leaves, and suffered major die-back to the main branches (Abbas et al., 2017).

5.3 Influences on species composition

The floral classification in the study area is notable for its absence of, or enormous decrease in tropical families, such as Rubiaceae, Myrtaceae, Malvaceae and Araliaceae, and several notable tropical rainforest species such as *Aporosa octandra*, *Sterculia lanceolata*, *Psychotria asiatica*, and in the higher elevation forests *Ardisia quinqueгона*, and *Acronychia pedunculata*..

Although environmental factors partially explained the species composition, it was interesting to note that topography (15%) and age of sites (29%) combined, explained 44% of the variation in species composition. The association of topography with species composition is also reported in the Xishuangbanna tropical forests in southwest China (Lan et al., 2011; Liu et al., 2014) and wet lowland tropical forest in Amazonian Ecuador (Valencia et al., 2004). In this study, elevation followed by stand-age remains the main determining factors of species composition, as elevation determines the major split between lowland and montane flora while stand-age explains the changes in species distribution along with the successional age classes. This means that the residual variation i.e. 44% of the variance, was not explained by either topography, soil or successional stage, indicating unknown influences on ecological processes. These may be attributed to deterministic variation resulting from unmeasured environmental constraints (Jones et al., 2008), spatially controlled biological processes limited by seed dispersal mechanisms (Lan et al., 2011) or by land use history (Bellemare et al., 2002)

6. Conclusions

Vegetation community data at species level from 28 sample sites were analyzed according to topography, soil and successional stage of forest stands. This presented a rare opportunity to analyse structural changes associated with biodiversity recovery in a tropical degraded landscape, over 70 years of forest regeneration. Results show that the stand basal area of secondary forest stands had only reached half that in the old-growth forest after 70 years of succession, which is attributed to soil nutrient loss following centuries of deforestation. The levelling off of species richness after 15 years of succession is indicative of the temporary co-existence of shade-intolerant, low growing pioneers, and shade-tolerant tall pioneers, the former becoming shaded out, while the latter progress to dominate the canopy after 50-year of succession. In Hong Kong, most of the forest has naturally regenerated along the

successional gradient from open ground to forest, on land which opportunely escaped the fire, since complete deforestation during WW2. Therefore the “new” forests mainly comprise species found in plots younger than 50 years and there is no evidence that this species composition is about to change in the near future if missing dispersal agents are not reintroduced. We found that elevation and stand age play major roles in the distribution of species, as 44% of the species variance was due to successional stage and topographic habitat association. Furthermore, unexplained variation in species composition suggests the underlying role of unmeasured environmental constraints such as spatially controlled biological processes limited by seed dispersal mechanisms (Karst et al., 2005; Lan et al., 2011). Especially, the absence of specialist forest fauna could pose a bottleneck in the continued succession and composition of this regenerating landscape, as late-successional, shade-tolerant forest trees have poor dispersal mechanisms. Although the secondary forests have now attained comparable or greater species richness than the patches of old-growth forest in the study area, their species composition is very different from these few old-growth forests stands. Almost all secondary forest sites lack the presence of late-successional tree species, such as *Cryptocaria chinensis* and *Sarcosperma laurinum* which can grow under shade. Similarly, large areas in the tropics and subtropics have been deforested in recent decades, resulting in impoverished vegetation communities, often lacking in sufficient seed sources for regeneration into highly biodiverse and stable ecosystems (MacDicken et al., 2015). In this case, to encourage natural succession as well as guarantee adequate genetic diversity in Hong Kong’s regenerating forests, strategic planting of climax trees should be undertaken, at locations near to the old-growth stands where the oldest forest pioneers are established. Thus, planting pockets of high diversity forest near the established forest patches would artificially enhance species diversity of the recovering forest in the landscape. The study also demonstrates the effectiveness of GIS-based analysis in understanding species-environmental relationships, for management and restoration of biodiversity in recovering tropical forests. Especially, spatial analysis can indicate suitable locations for high biodiversity pockets for rapid recovery of degraded tropical forest. Future studies will further increase understanding of the patterns and processes of secondary forest recovery by increasing the number of field sampling sites, as well as by extending geographic coverage of the landscape to avoid sampling error and exclusion of certain species.

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